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Research Article

Nutrient enrichment and artificial light at night synergistically confer a competitive advantage to alien aquatic species over natives

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Abstract

Many freshwater ecosystems are currently facing the dual challenges of artificial light at night (ALAN) and nutrient enrichment. How these simultaneously acting environmental factors affect competitive outcomes between alien and native aquatic plants has not been thoroughly investigated. Here, we conducted a greenhouse experiment to quantify the competitive outcomes and their determinants of nine pairs of alien and native aquatic plant species in China under fully crossed factorial combinations of ALAN (Ambient vs. ALAN) and nutrient enrichment (Low vs. High). Nutrient enrichment significantly affected competitive outcomes. Specifically, native species tended to have more biomass under low-nutrient conditions, while the reverse was true under high-nutrient, although the trends were not significant. This pattern was even more pronounced in the presence of ALAN. Differential effects of nutrient enrichment and ALAN on interspecific competition of alien and native species may be responsible for variation in competitive outcomes. We found that nutrient enrichment tended to increase the interspecific competition coefficients for native species, whereas an opposite trend for alien species was observed, this effect being most prominent in the presence of ALAN. Our findings suggest that nutrient enrichment and ALAN could synergistically confer a competitive advantage to alien species over native species. Therefore, intervention measures are necessary to minimise nutrient enrichment of freshwater habitats, especially in habitats exposed to light pollution resulting from ALAN.

Key words: Artificial light at night, competitive outcome, freshwater ecosystem, intra- and interspecific competition, intrinsic growth rates, nutrient availability, plant invasion

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Introduction

The Anthropocene is characterised by the widespread invasion of alien plants, posing threats to local biodiversity, disrupting ecosystem services and causing substantial economic losses (Vilà et al. 2011; Schaffner et al. 2020; Diagne et al. 2021; Zhang et al. 2023b). The success of these invasions hinges on competitive interactions between alien and native species (Funk and Vitousek 2007; Pearse and Altermatt 2013; Wang et al. 2017). It is hypothesised that alien species are generally more competitive than native species, a notion supported by meta-analyses primarily focusing on interspecific competition intensity (Kuebbing and Nuñez 2016; Golivets and Wallin 2018). However, intrinsic growth rates and intraspecific competition intensity also significantly affect the competitive outcomes (Chesson 2000; Hart et al. 2018). Thus, predicting co-existence dynamics between native and alien species requires consideration of all three determinants: intrinsic growth

rates, intra- and interspecific competition. Yet, studies integrating these factors comprehensively remain limited (but see Godoy et al. (2014); Godoy and Levine (2014); Chu and Adler (2015); Zhang and van Kleunen (2019)).

In theory, species with higher intrinsic growth rates and lower intra- and interspecific competition intensity are expected to outcompete others (Zhang and van Kleunen 2019). However, in reality, these determinants may not operate independently. Alien species often exhibit higher intrinsic growth rates, but this can coincide with stronger intraspecific competition (Dostál et al. 2019). Furthermore, there is a trade-off between intra- and interspecific competitive abilities, observed in some alien plant species (Lankau and Strauss 2007; Lankau 2009). For instance, in environments where an alien species faces intense intraspecific competition due to high abundance, individuals may prioritise enhancing intraspecific competitive ability, potentially at the expense of reduced competitive ability against other species (Lankau 2008). Therefore, accurately predicting species co-existence remains a significant challenge.

Ecosystems worldwide are currently undergoing unprecedented environmental changes driven by factors such as nutrient enrichment (Sinha et al. 2017). Nutrient enrichment can potentially amplify the competitive advantage of alien plant species over native ones. For example, garden experiments with individual plants have demonstrated that alien species derive greater benefits from increased resource availability compared to native species (Liu and van Kleunen 2017; Kawawa Abonyo and Oduor 2024; Shan et al. 2024). Therefore, nutrient enrichment may alter competitive outcomes by impacting the disparity in intrinsic growth rates between alien and native species. Studies also indicate that nutrient enrichment reduces the competitive effects of native species on aliens (Barger et al. 2003; Eller and Oliveira 2017; Sun et al. 2023), although this often reflects changes in relative differences between intra- and interspecific competition (but see Slate et al. (2022)). Additionally, nutrient enrichment significantly reduces intraspecific competition intensity for alien species, while increasing it for native species (Ba and Facelli 2022). It remains unclear whether this pattern persists in the presence of interspecific competition. Integrating intrinsic growth rates, intra- and interspecific competition provides deeper insights into how nutrient enrichment influences competitive outcomes between alien and native species. In addition, the current understanding of these effects of nutrient enrichment is mainly from terrestrial ecosystems, while little is known about the situation in aquatic habitats.

Artificial light at night (ALAN) imposes significant anthropogenic pressure on natural biological systems (Falchi et al. 2016; Kyba et al. 2017; Sanders et al. 2021). ALAN affects not only animal behaviour, physiology and life histories, but also alters plant community composition and phenology (Bennie et al. 2016; Liu et al. 2022). Recent field surveys by Murphy et al. (2021) have found a positive correlation between the presence of the invasive plant *Bromus tectorum* L. and streetlights, suggesting that ALAN may differently influence alien and native species, thereby affecting their competitive outcomes. However, Speißer et al. (2021) found no evidence that ALAN enhances the dominance of alien species in communities. Moreover, they observed a trend of decreased fitness of alien species under ALAN compared to ambient light conditions when grown individually. Conversely, another study suggested that ALAN tended to promote the growth of alien species under monocultures (Liu et al. 2022). Intraspecific interactions may partially explain the discrepancies between these studies' results. Overall, our understanding of how ALAN impacts the performance of invasive and native species, as well as their intra- and interspecific interactions, remains limited.

A large number of exotic aquatic plants have been consciously introduced for ecological restoration and landscape creation and many aquatic habitats have suffered severe plant invasions as a result (Hussner et al. 2021; Wang et al. 2024). In addition, freshwater ecosystems are particularly susceptible to ALAN because lighting road networks, urban development and industrial infrastructure are often located along rivers, lakes and coasts (Reid et al. 2019; Segrestin et al. 2021), while industrial wastewater and storm-water runoff from urban areas simultaneously contribute to nutrient enrichment (Maharjan et al. 2022; Kawawa Abonyo and Oduor 2024). Thus, aquatic habitats provide an ideal site for us to test the interactive effects of ALAN and nutrient enrichment.

Here, we conducted experiments using a freshwater model system with seven alien and six native species. Employing a response surface design (Inouye 2001) in which we varied the density of both species of a pair independently, we planted 4320 individuals, describing competitive relationships between nine pairs of alien and native aquatic species under fully crossed factorial combinations of ALAN and nutrient enrichment treatments, each at two levels. We tested: (1) whether alien aquatic species are more competitive than native species and (2) how nutrient enrichment and ALAN affect competitive outcomes between alien and native aquatic species.

Materials and methods

Study species

To examine the effects of ALAN and nutrient enrichment on competitive outcomes between alien and native aquatic plants, we selected seven alien and six native species to create nine species pairs (Suppl. material 1: table S1). The alien species we used in the experiment included all of China's invasive submerged and floating plants, except for *Azolla filiculoides* Lam. (Wang et al. 2019; Wu and Ding 2019), which increased the generalisability of the results (van Kleunen et al. 2014). Species pairs were chosen, based on their co-occurrence in habitats and differences in growth forms. *Hydrocharis dubia* (Blume) Backer, *Pistia stratiotes* L., *Cabomba caroliniana* A.Gray, *Egeria densa* (Planch.) Casp., *Elodea nuttallii* (Planch.) H.St. John and *Pontederia crassipes* Mart. were sourced from commercial plant traders, while the remaining species were collected from pools of water from cement tanks at the National Field Station of Freshwater Ecosystems of Liangzi Lake, Hubei Province, China (30°15'N, 114°33'E)(hereafter referred to as the "Liangzi Lake Station"). Before starting the experiment, we selected 240 individuals of similar size for each species. As three species were used in multiple pairs, the actual number of individuals was 240*n, where n represents the number of repetitions.

Experimental set-up

The experiment was conducted in the greenhouse at the Liangzi Lake Station, China. For each alien-native species pair, we transplanted individual plants according to a response-surface experimental design (Inouye 2001). This design included 15 different density combinations, with total densities of 4, 8 or 12 plants per pot and the frequency of each species from 0 via 0.25, 0.5 and 0.75 to 1. Each density combination for each species pair was replicated 4 times and then randomly assigned to a fully crossed factorial combination of ALAN and nutrient enrichment treatments at two levels each (Fig. 1).

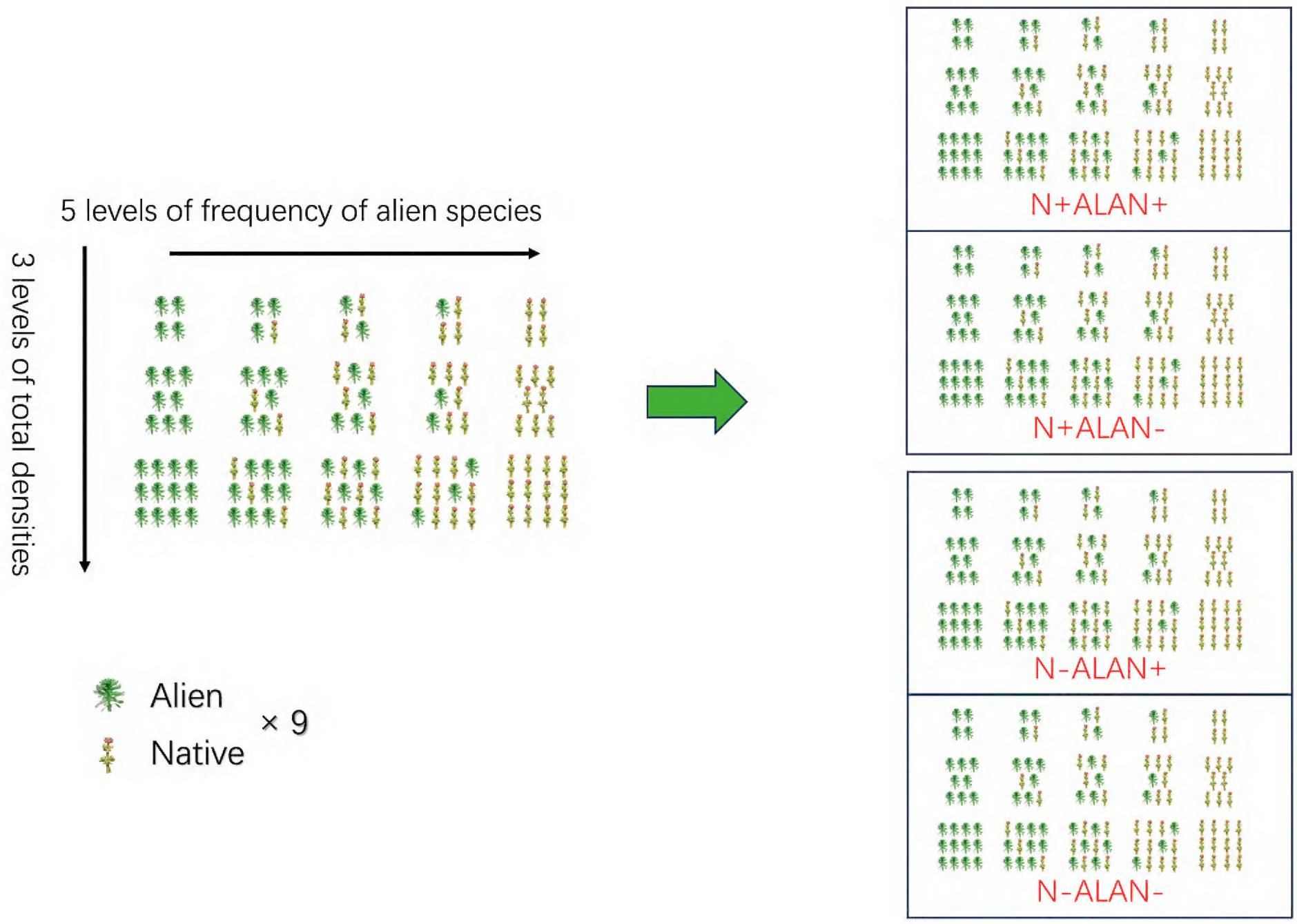

Figure 1. Graphical illustration of the response-surface design used for each pair of alien and native aquatic plant species. Each pair is treated with different nutrient (N– vs. N+) and ALAN (ALAN– vs. ALAN+) conditions.

Due to differences in growth periods and growth forms amongst different species, the experimental duration and the type of containers were varied. On 12, 13 March 2024, we transplanted the individuals of the first six species pairs into soil-filled plastic pots (top diameter: 18 cm, bottom diameter: 13 cm, height: 12.5 cm) according to the experimental design. The soil (TN: 0.60 ± 0.005 g kg^{-1}, TP: 0.58 ± 0.03 g kg^{-1}, mean ± standard error (SE), n = 3) was obtained from the Liangzi Lake Station and meticulously sieved to eliminate stones, plants and animal remnants. We opted for terrestrial topsoil as opposed to lake-bottom silt, in order to mitigate the potential for the emergence of unwanted macrophytes stemming from an aquatic plant seed bank (Yan et al. 2024). We then placed six pots of the same density combination and treatment in a specific order in a rectangular aquarium (length × width × height: 105 × 50 × 60 cm), arranged in three rows and two columns and filled the aquarium with lake water to a depth of 50 cm. On 4 April 2024, we placed the individuals of the 7^{th} and 8^{th} species pairs in cylindrical stainless-steel tanks (50 cm diameter, 60 cm height) with lake water depth of 50 cm according to the experimental design. On the same day, we placed the individuals of the 9^{th} species pair in circular flower pots (70 cm top diameter, 50 cm bottom diameter, 40 cm height) with a water depth of 30 cm.

After three days of transplanting the individuals, we started different experimental treatments. We used LED strips fixed above the three types of containers to simulate ALAN. The LED strips (6 W/m, IP 180 lm/m, warm white 3300K-5000K; NVC,

China) were positioned 10 cm above the water surface for the rectangular aquarium, 56 cm for the cylindrical stainless-steel tanks and 40 cm for the circular flower pots. The containers were arranged in rows, with the plastic pots in the rectangular aquarium also arranged in rows. Therefore, the LED strips fixed in the middle of the two rows of cylindrical stainless-steel tanks, the two rows of circular flower pots and the single row of rectangular aquariums provided uniform illumination for each container. At night, the control group remained in darkness, while the ALAN group was continuously exposed to light at an intensity of 16 ± 3.5 lux. During the experiment, the LED lights were switched on at 6:30 pm and off at 6:30 am the next day.

We controlled the nutrient levels by varying the amount of slow-release fertiliser (Osmocote Plus 15N-9P-12K+2MgO+TE, Everris). Specifically, we added 2.3 g of fertiliser to half of the rectangular aquariums for high nutrient treatment, leaving the other half without fertiliser for low nutrient treatment. For the cylindrical stainless-steel tanks and circular flower pots, the high nutrient treatment involved adding 7 g and 1.6 g of fertiliser, respectively, while the low nutrient treatment involved adding 2.5 g and 0.7 g, respectively. The controlled release fertiliser was placed in a mesh bag at the bottom of the container. For the rectangular aquariums, the nutrient concentrations in the water column under low and high nutrient treatments were 0.758 ± 0.025 mg l^{-1} and 0.967 ± 0.022 mg l^{-1} for TN, 0.014 ± 0.001 mg l^{-1} and 0.030 ± 0.001 mg l^{-1} for TP, respectively. For the cylindrical stainless-steel tanks and circular flower pots, the nutrient concentrations in the water column under low and high nutrient treatments were 1.236 ± 0.077 mg l^{-1} and 1.476 ± 0.080 mg l^{-1} for TN, 0.141 ± 0.016 mg l^{-1} and 0.222 ± 0.030 mg l^{-1} for TP, respectively. Data represent mean values ± standard error, n = 18. These two water quality indices were significantly different between the two nutrient levels. The concentration of nutrients in the high nutrient treatment was within the range of nutrient enrichment in freshwater lakes across China (Huo et al. 2013).

Measurements

On 5 May 2024, we harvested all plants from the rectangular aquarium, dried each individual (including roots) to a constant weight at 70 °C and weighed them to the nearest milligram. On 20 May 2024, we harvested, dried and weighed the remaining plants in the same manner.

Statistical analyses

Intrinsic growth rates and competition coefficients

To describe the competition between alien and native species pairs, we fitted our data on the biomass of individual plants to a linearised version of a modified Ricker competition model (Ricker 1954) by taking the natural log of both sides of the equation:

$$\ln(B_{i,t}) = \ln(\lambda_i) - \alpha_{ii} N_{i,t} - \alpha ij\, N_{j,t}$$

In the equation, $B_{i,t}$ is the individual biomass of species i in year t. $N_{i,t}$ and $N_{j,t}$ are the number of individuals of species i and j in year t, respectively. λi is the intrinsic growth rate of species i, which represents the expected biomass of an individual in the absence of conspecific and heterospecific neighbours. α_{ii} represents

the per capita effect of species *i* on itself (the intraspecific competition coefficient) and α_{ij} represents the per capita effect of species *j* on species *i* (the interspecific competition coefficient). Positive values of competition coefficients indicate competition amongst individuals and negative values indicate facilitation. $B_{i,t}$,$N_{i,t}$ and $N_{j,t}$ were measured directly during the experiment, while λi, α_{ii} and α_{ij} were estimated by fitting the linearised model. Although the subscript *t* typically denotes a time step (e.g. in years), here it refers only to the single time point of harvest at the end of the experiment and does not represent inter-annual dynamics.

For each species pair under the four different experimental conditions, we fitted a linear mixed-effects model. We used total biomass of each individual at the end of the experiment. We included the number of conspecific and heterospecific competitors as fixed effects, with container as a random effect to account for non-independence of individuals within the same container. We used the number of individuals at the end of experiment rather than at the beginning of the experiment.

Next, we used linear mixed-effects models to test the effects of species status, nutrient enrichment and ALAN on intrinsic growth rates and intraspecific competition coefficients. We included species status, nutrient enrichment, ALAN and their interactions as fixed factors, with identity (nested within family) of target species as random effects. We also tested the effects of species status, nutrient enrichment and ALAN on interspecific competition coefficients. In this mixed-effects linear model, we included species status, nutrient enrichment, ALAN and their interactions as fixed factors, with target species and competitor species (nested within their respective families) as random effects. In all models, we included the inverse of variance as weights.

Competitive outcomes

Based on population-level biomass, we calculated $\ln RR_k$, the competitive outcome between alien and native plants in each of the biculture containers (*k*) as:

$$\ln RRk = \ln(TB_{k_a)} - \ln (TB_{k_n})$$

where TB_{k_a} and TB_{k_n} are the total biomass of alien and native species, respectively, in the biculture container *k*. Subsequently, for each pair of species in different conditions, we used a linear model with $\ln RR_k$ as the response variable and an intercept as the only explanatory variable. Therefore, a positive intercept value fitted for a pair signifies that, on average, the alien species in that pair exhibited higher biomass than the native species across a broad range of density combinations (indicating greater competitiveness of the alien species), whereas a negative intercept value indicates the opposite.

To test how nutrient enrichment and ALAN affect competitive outcomes between alien and native species, we fitted a linear mixed-effects model. The model included nutrient enrichment, ALAN and their interactions as fixed factors, with identity (nested within family) of native species as random effects. We also included identity of alien species as random effects and we allowed each alien species to respond differently to the nutrient treatments (i.e. we included random slopes). We included the inverse of variance of competition outcomes as weights.

Considering potential differences between species combinations, we also fitted a linear model using the *gls* function. This model included nutrient enrichment, ALAN, identity of species pair and their interactions as fixed factors. Additionally, it allowed for different variances for each species pair.

All analyses were conducted using the lme4 package (Bates et al. 2015) and nlme package (Pinheiro et al. 2023) in R 4.2.0 (Team 2022). Results were visualised using the *plot* function or the *ggplot* function from the ggplot2 package (Wickham 2016).

Results

Compared with native aquatic species, alien species tended to have higher intrinsic growth rates, but the difference was not statistically significant (Table 1, Fig. 2a). The intrinsic growth rate was also not affected by the interaction between status and nutrient enrichment or the interaction between status and ALAN (Table 1, Fig. 2a). Alien species tended to have lower intraspecific competition coefficients compared with native aquatic species, but the difference was not statistically significant (Table 1, Fig. 2b). The intraspecific competition coefficients were also not affected by the interaction between status and nutrient enrichment or the interaction between status and ALAN (Table 1, Fig. 2b). Overall, there was no difference in interspecific competition coefficients between alien and native species (Table 1, Fig. 2c). However, nutrient enrichment affected the interspecific competition coefficients of alien and native species significantly differently (Table 1). Specifically, nutrient enrichment tended to increase the interspecific competition coefficients for native species, whereas an opposite trend was observed for alien species (Suppl. material 1: fig. S1), this effect being most pronounced in the presence of ALAN (a marginally significant three-way interaction between status, nutrient and ALAN in Table 1, Fig. 2c).

Overall, when grown together, alien species and native species exhibited similar biomass (Fig. 3). Competitive outcomes between alien and native species were significantly affected by nutrient enrichment (Table 2). Specifically, under low-nutrient conditions, native species tended to have higher biomass, while under high-nutrient conditions, alien species tended to have higher biomass (Fig. 3). However, these trends were not statistically significant. This pattern was more pronounced

Table 1. Effects of status of target species (native vs. alien), nutrient enrichment (low-nutrient vs. high-nutrient levels), ALAN treatment (ambient vs. ALAN) and their interaction on intrinsic growth rates (λ_i) and intra- and interspecific competition coefficients (α_{ii} and α_{ij}). Significant ($P < 0.05$) effects are in bold. Marginally significant ($0.05 \leq P < 0.10$) effects are shown in italics. The significance of fixed effects was assessed with likelihood-ratio tests by comparing models with and without the effect of interest.

	λ_i; χ^2	*P*	α_{ii}; χ^2	*P*	α_{ij}; χ^2	*P*
Status (S)	1.521	0.217	1.902	0.168	0.613	0.433
Nutrient (N)	0.542	0.462	1.137	0.286	1.688	0.193
ALAN (L)	1.305	0.253	0.014	0.906	0.765	0.381
S × N	1.439	0.23	1.479	0.224	5.503	**0.018**
S × L	0.821	0.364	0.063	0.802	0.578	0.446
N × L	4.653	**0.031**	2.831	*0.093*	0.389	0.532
S × N × L	1.031	0.309	1.399	0.237	3.385	*0.065*
Random effects	SD		SD		SD	
Species of target	0.906		0.000		0.009	
Family of target	0.503		0.019		0.013	
Species of competitor	-		-		0.019	
Family of competitor	-		-		0.002	
Residual	0.407		0.450		0.280	
	R^2_m	R^2_c	R^2_m	R^2_c	R^2_m	R^2_c
	0.080	0.877	0.001	0.003	0.003	0.011

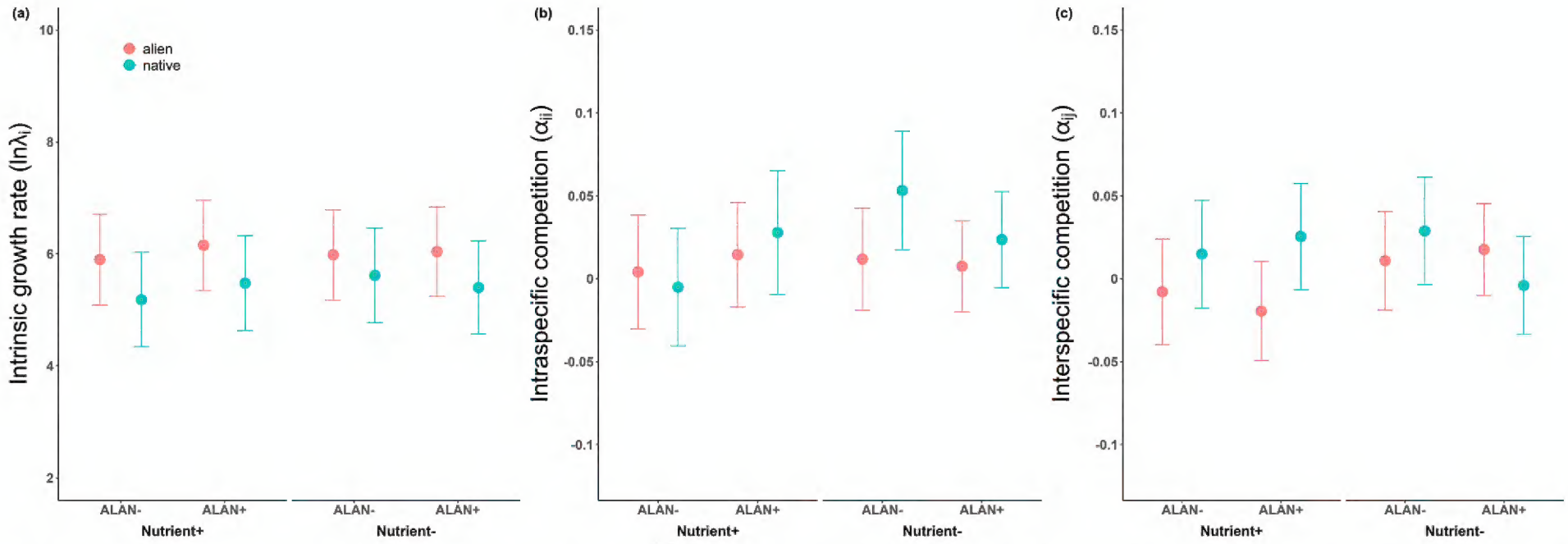

Figure 2. Mean intrinsic growth rates (**a** λ_i) and intra- and interspecific competition coefficients (**b** α_{ii}; **c** α_{ij}) for alien and native aquatic plant species under different experimental treatments. Positive values of α_{ii} and α_{ij} indicate competitive interactions. Error bars represent 95% confidence intervals. Intrinsic growth rates (λi), whose unit is milligram, was natural log-transformed.

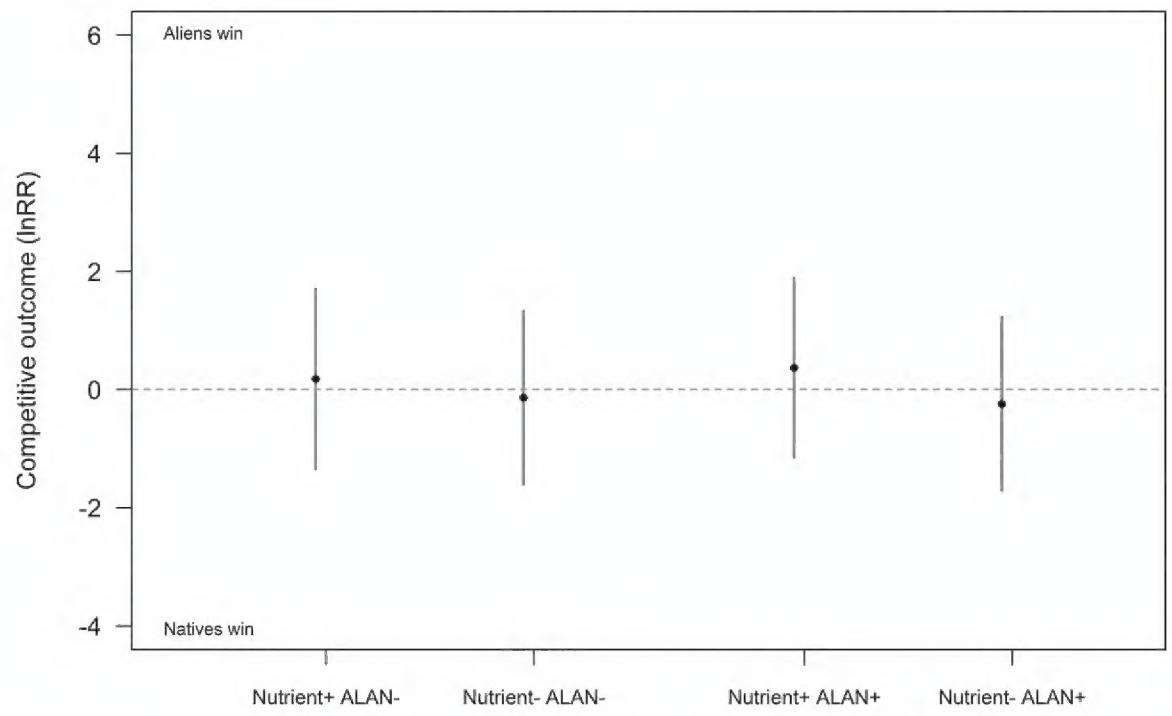

Figure 3. Mean values of competitive outcomes between alien and native plant species (i.e. mean values of $\ln RR_k$) under different experimental treatments. Error bars represent 95% confidence intervals.

Table 2. Effects of nutrient enrichment (low-nutrient vs. high-nutrient levels), ALAN treatment (ambient vs. ALAN) and their interaction on competitive outcomes (i.e. which species have higher biomass in bicultures across different density combinations). Significant ($P < 0.05$) effects are in bold. Marginally significant ($0.05 \leq P < 0.10$) effects are shown in italics. The significance of fixed effects was assessed with likelihood-ratio tests by comparing models with and without the effect of interest.

	χ^2	*P*
Nutrient (N)	4.524	**0.033**
ALAN (L)	0.255	0.614
N × L	4.008	**0.045**
Random effects	SD	
Alien species	1.050 (0.260)[a]	
Native species	0.457	
Family of native	1.231	
Residual	0.211	
	R^2_m	R^2_c
	0.022	0.984

[a]Here, the standard deviations (SD) are given for the random intercepts (corresponding to the values in the high nutrient treatment) and random slopes (corresponding to the effects of the low nutrient treatment) of species of alien. The values in brackets represent the SDs of the random slopes.

in the presence of ALAN, demonstrated by a significant ALAN × nutrient enrichment interaction (Table 2, Fig. 3). We also found that competitive outcomes were significantly affected by species combination (Suppl. material 1: table S2, fig. S2). Moreover, the effect (Suppl. material 1: table S2, fig. S2) and determinants (Suppl. material 1: figs S3–S5) of nutrient enrichment on competitive outcomes varied amongst different species combinations.

Discussion

While alien species are often perceived as more competitive than native counterparts (Vilà and Weiner 2004; Pearse et al. 2019), our study did not find significant differences in competitive ability between them (Fig. 3). Similarly, Zhang and van Kleunen (2019) found in their study quantifying competition outcomes amongst 48 pairs of native and naturalised alien plants in Germany that alien and native species generally exhibited comparable competitive abilities. However, their research indicated that common alien plants were more competitive than rare natives. Previous studies into alien-native competition may have been skewed towards using rare native species (Vilà and Weiner 2004), potentially contributing to variable outcomes. The native aquatic species in our study are widely distributed in China and some are recognised as invasive in other regions worldwide (e.g. *Myriophyllum spicatum* L. (Marko et al. 2008; Martin and Coetzee 2014), *Potamogeton crispus* L. (Fleming et al. 2015), *Hydrilla verticillata* (L.f.) Royle (Louback-Franco et al. 2020; Mormul et al. 2020). A meta-analysis previously indicated no significant trait disparities between invasive alien and native species known to be invasive elsewhere (Van Kleunen et al. 2010). Thus, our findings, alongside existing research, suggest that alien species do not inherently possess a competitive advantage over commonly encountered natives.

Growth and intraspecific competition may exhibit a trade-off relationship, where larger and faster-growing species typically face stronger resource competition and greater negative density dependence (Dostál et al. 2019). However, our study did not observe this trade-off pattern. Instead, we found that alien species generally displayed higher intrinsic growth rates coupled with lower, rather than higher, levels of intraspecific competition (Fig. 2a, b). Future research should investigate the prevalence and mechanisms underlying this relationship between growth and intraspecific competition. In contrast to findings from several meta-analyses (Kuebbing and Nuñez 2016; Golivets and Wallin 2018), we did not find evidence that alien species consistently exhibit lower interspecific competition coefficients compared to natives (Fig. 2c). Potential explanations include the smaller sample size of species pairs in our study compared to meta-analyses, resulting in reduced statistical power. Moreover, the intensity of interspecific competition between alien and native species may vary depending on environmental conditions (e.g. nutrient availability), a factor that our study's limited environmental scope may not fully capture. Last, data from several meta-analyses may have been derived primarily from terrestrial ecosystems, whereas the subjects of our study were submerged and floating aquatic plants.

Previous empirical studies examining the effects of nutrient enrichment on competitive outcomes have produced mixed results. While some studies indicate positive effects (Zhang et al. 2017; Uddin and Robinson 2018; Ren et al. 2019), others suggest that in the presence of common natives, nutrient enrichment may not affect or could even diminish the competitive advantage of alien species (Going et al. 2009;

Liu et al. 2016; Yan et al. 2024). Moreover, trophic interactions can mediate the effects of nutrient enrichment on competitive outcomes. For instance, recent research by Zhang et al. (2023a) demonstrated that increased nutrient availability suppressed the dominance of alien species in pots inoculated with active soil microbiota, but not in those lacking soil microbes. Here, we show that nutrient enrichment may favour the invasion of alien aquatic plants. More importantly, we found that the positive effects of nutrient enrichment were more pronounced in the presence of ALAN. In other words, nutrient enrichment and ALAN synergistically conferred a competitive advantage to alien species over native species.

Intrinsic growth rates play a pivotal role in shaping competitive outcomes, often outweighing the effects of intra- and interspecific competition (Zhang and van Kleunen 2019). However, we did not find that the effects of nutrient enrichment on competitive outcomes were driven by intrinsic growth rates (Fig. 2a). Specifically, nutrient enrichment did not alter the intrinsic growth rates of either alien or native species. One possible explanation is that plants in nutrient-rich environments tend to be more nutritious (Deng et al. 2017; Sardans et al. 2017; Oldroyd and Leyser 2020) and often reduce secondary metabolite concentrations (Jamieson et al. 2017; Li et al. 2022), making them more favourable to herbivores. Nonetheless, the biomass increase induced by nutrient enrichment compensates for tissue losses from herbivory. Moreover, while nutrient enrichment initially suppresses early growth of both alien and native species by promoting algal growth (higher chlorophyll a, $p < 0.001$), it subsequently facilitates rapid growth.

For interspecific competition, there were significant differences in the responses of alien and native plants to nutrient enrichment. More importantly, we found tentative evidence that ALAN moderates the effects of nutrient enrichment on interspecific competition between alien and native plants. Specifically, the competitive effects of native species on alien species tended to be negative under low-nutrient conditions, but shifted to tending to be positive under high-nutrient conditions (Suppl. material 1: fig. S1). Although these trends are not statistically significant, this partially supports previous predictions that, in environments with high biological pressures, neighbouring organisms can ameliorate these pressures, thereby highlighting the importance of facilitation, whereas under less stressful biological conditions, competition becomes more prominent, a pattern confirmed across various communities (Bertness and Callaway 1994; Milchunas and Noy-Meir 2002; Callaway et al. 2005; Alberti et al. 2008). The effect of nutrient enrichment was more pronounced in the presence of ALAN (Fig. 2c), which may be attributed to the fact that ALAN intensifies the competition for nutrients between native plants and algae on the one hand and competition for resources (e.g. light, nutrients) between native and alien plants on the other hand. Interestingly, the interspecific mutualism was not mutual i.e. the alien species did not promote the natives at high nutrient levels (Suppl. material 1: fig. S1). This may mean that, although the presence of alien species may indirectly promote the growth of native species by inhibiting algae (Le Bagousse-Pinguet et al. 2012), it also reduces the resource availability of native species through direct competition.

Importantly, we observed significant variations in competitive outcomes amongst different species combinations (Suppl. material 1: fig. S2). While some alien species exhibited greater competitive ability than natives, others demonstrated comparable or lower competitive ability. Moreover, plant responses to nutrient enrichment were species-specific (Suppl. material 1: fig. S2), suggesting that nutrient enrichment does not

universally enhance the competitive ability of alien species. However, it should be noted that some malignant invaders, such as *Pontederia crassipes* Mart., are more competitive than native co-existing species and benefit more from nutrient enrichment. Therefore, regulatory attention should be focused on such species. As plant competitive advantage and responses to nutrient enrichment are influenced by functional traits that dictate resource-use strategies (Hou and Wang 2023; Shan et al. 2023), our study underscores the importance of functional traits related to resource use strategies over invasion status in determining competitive outcomes and responses to nutrient changes.

In conclusion, our study found that nutrient enrichment and ALAN can act synergistically to shift the competitive balance in favour of alien species. Although similar phenomena have been observed in terrestrial ecosystems (Kawawa Abonyo and Oduor 2024), our findings in freshwater ecosystems are still insightful because they reveal patterns and processes may be different from those in terrestrial environments. Nonetheless, we observed that alien aquatic species are not more competitive than common natives.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

JZ conceived the idea. JZ and CL designed the experiment, JZ, YN, YZ and FL conducted the experiment. JZ analysed the data. JZ wrote the manuscript with input from HY and CL. All au-thors approved the submission to the journal.

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Alberti J, Escapa M, Iribarne O, Silliman B, Bertness M (2008) Crab herbivory regulates plant facilitative and competitive processes in argentinean marshes. Ecology 89(1): 155–164. https://doi.org/10.1890/07-0045.1

Ba L, Facelli J (2022) Invasive success of exotic wild oat depends on nutrient availability and competition in temperate grasslands of southern Australia. Plant and Soil 472(1): 465–478. https://doi.org/10.1007/s11104-021-05262-8

Barger N, D'Antonio C, Ghneim T, Cuevas E (2003) Constraints to colonization and growth of the African grass, Melinis minutiflora, in a Venezuelan savanna. Plant Ecology 167(1): 31–43. https://doi.org/10.1023/A:1023903901286

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01

Bennie J, Davies T, Cruse D, Gaston K (2016) Ecological effects of artificial light at night on wild plants. Journal of Ecology 104(3): 611–620. https://doi.org/10.1111/1365-2745.12551

Bertness M, Callaway R (1994) Positive interactions in communities. Trends in Ecology & Evolution 9(5): 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Callaway R, Kikodze D, Chiboshvili M, Khetsuriani L (2005) Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology 86(7): 1856–1862. https://doi.org/10.1890/04-0784

Chesson P (2000) Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31: 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Chu C, Adler P (2015) Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. Ecological Monographs 85(3): 373–392. https://doi.org/10.1890/14-1741.1

Deng Q, Hui D, Dennis S, Reddy K (2017) Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: A meta-analysis. Global Ecology and Biogeography 26(6): 713–728. https://doi.org/10.1111/geb.12576

Diagne C, Leroy B, Vaissière A, Gozlan R, Roiz D, Jarić I, Salles J, Bradshaw C, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592(7855): 571–576. https://doi.org/10.1038/s41586-021-03405-6

Dostál P, Tasevová K, Klinerová T (2019) Linking species abundance and overyielding from experimental communities with niche and fitness characteristics. Journal of Ecology 107(1): 178–189. https://doi.org/10.1111/1365-2745.13005

Eller C, Oliveira R (2017) Effects of nitrogen availability on the competitive interactions between an invasive and a native grass from Brazilian cerrado. Plant and Soil 410(1): 63–72. https://doi.org/10.1007/s11104-016-2984-0

Falchi F, Cinzano P, Duriscoe D, Kyba C, Elvidge C, Baugh K, Portnov B, Rybnikova N, Furgoni R (2016) The new world atlas of artificial night sky brightness. Science Advances 2(6): e1600377. https://doi.org/10.1126/sciadv.1600377

Fleming J, Dibble E, Madsen J, Wersal R (2015) Investigation of Darwin's naturalization hypothesis in invaded macrophyte communities. Biological Invasions 17(5): 1519–1531. https://doi.org/10.1007/s10530-014-0812-0

Funk J, Vitousek P (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446(7139): 1079–1081. https://doi.org/10.1038/nature05719

Godoy O, Levine J (2014) Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory. Ecology 95(3): 726–736. https://doi.org/10.1890/13-1157.1

Godoy O, Kraft N, Levine J (2014) Phylogenetic relatedness and the determinants of competitive outcomes. Ecology Letters 17(7): 836–844. https://doi.org/10.1111/ele.12289

Going B, Hillerislambers J, Levine J (2009) Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. Oecologia 159(4): 839–847. https://doi.org/10.1007/s00442-008-1264-y

Golivets M, Wallin K (2018) Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. Ecology Letters 21(5): 745–759. https://doi.org/10.1111/ele.12934

Hart S, Freckleton R, Levine J (2018) How to quantify competitive ability. Journal of Ecology 106(5): 1902–1909. https://doi.org/10.1111/1365-2745.12954

Hou M, Wang J (2023) Functional traits of both specific alien species and receptive community but not community diversity determined the invasion success under biotic and abiotic conditions. Functional Ecology 37(10): 2598–2610. https://doi.org/10.1111/1365-2435.14411

Huo S, Ma C, Xi B, Su J, Zan F, Ji D, He Z (2013) Establishing eutrophication assessment standards for four lake regions, China. Journal of Environmental Sciences 25(10): 2014–2022. https://doi.org/10.1016/S1001-0742(12)60250-2

Hussner A, Heidbüchel P, Coetzee J, Gross E (2021) From introduction to nuisance growth: A review of traits of alien aquatic plants which contribute to their invasiveness. Hydrobiologia 848(9): 2119–2151. https://doi.org/10.1007/s10750-020-04463-z

Inouye B (2001) Response surface experimental designs for investigating interspecific competition. Ecology 82(10): 2696–2706. https://doi.org/10.1890/0012-9658(2001)082[2696:RSEDFI]2.0.CO;2

Jamieson M, Burkle L, Manson J, Runyon J, Trowbridge A, Zientek J (2017) Global change effects on plant–insect interactions: The role of phytochemistry. Current Opinion in Insect Science 23: 70–80. https://doi.org/10.1016/j.cois.2017.07.009

Kawawa Abonyo C, Oduor A (2024) Artificial night-time lighting and nutrient enrichment synergistically favour the growth of alien ornamental plant species over co-occurring native plants. Journal of Ecology 112(2): 319–337. https://doi.org/10.1111/1365-2745.14235

Kuebbing S, Nuñez M (2016) Invasive non-native plants have a greater effect on neighbouring natives than other non-natives. Nature Plants 2(10): 16134. https://doi.org/10.1038/nplants.2016.134

Kyba C, Kuester T, Sánchez de Miguel A, Baugh K, Jechow A, Hölker F, Bennie J, Elvidge C, Gaston K, Guanter L (2017) Artificially lit surface of Earth at night increasing in radiance and extent. Science Advances 3(11): e1701528. https://doi.org/10.1126/sciadv.1701528

Lankau R (2008) A chemical trait creates a genetic trade-off between intra- and interspecific competitive ability. Ecology 89(5): 1181–1187. https://doi.org/10.1890/07-1541.1

Lankau R (2009) Genetic Variation Promotes Long-Term Coexistence of Brassica nigra and Its Competitors. American Naturalist 174(2): E40–E53. https://doi.org/10.1086/600083

Lankau R, Strauss S (2007) Mutual Feedbacks Maintain Both Genetic and Species Diversity in a Plant Community. Science 317(5844): 1561–1563. https://doi.org/10.1126/science.1147455

Le Bagousse-Pinguet Y, Liancourt P, Gross N, Straile D (2012) Indirect facilitation promotes macrophyte survival and growth in freshwater ecosystems threatened by eutrophication. Journal of Ecology 100(2): 530–538. https://doi.org/10.1111/j.1365-2745.2011.01931.x

Li Y, Gao Y, van Kleunen M, Liu Y (2022) Herbivory may mediate the effects of nutrients on the dominance of alien plants. Functional Ecology 36(5): 1292–1302. https://doi.org/10.1111/1365-2435.14019

Liu Y, van Kleunen M (2017) Responses of common and rare aliens and natives to nutrient availability and fluctuations. Journal of Ecology 105(4): 1111–1122. https://doi.org/10.1111/1365-2745.12733

Liu L, Quan H, Dong B, Bu X, Li L, Liu F, Lei G, Li H (2016) Nutrient enrichment alters impacts of Hydrocotyle vulgaris invasion on native plant communities. Scientific Reports 6(1): 39468. https://doi.org/10.1038/srep39468

Liu Y, Speißer B, Knop E, van Kleunen M (2022) The Matthew effect: Common species become more common and rare ones become more rare in response to artificial light at night. Global Change Biology 28(11): 3674–3682. https://doi.org/10.1111/gcb.16126

Louback-Franco N, Dainez-Filho M, Souza D, Thomaz S (2020) A native species does not prevent the colonization success of an introduced submerged macrophyte, even at low propagule pressure. Hydrobiologia 847(7): 1619–1629. https://doi.org/10.1007/s10750-019-04116-w

Maharjan A, Groffman P, Vörösmarty C, Tzortziou M, Tang X, Green P (2022) Sources of terrestrial nitrogen and phosphorus mobilization in South and South East Asian coastal ecosystems. Watershed Ecology and the Environment 4: 12–31. https://doi.org/10.1016/j.wsee.2021.12.002

Marko M, Gross E, Newman R, Gleason F (2008) Chemical profile of the North American native Myriophyllum sibiricum compared to the invasive M. spicatum. Aquatic Botany 88(1): 57–65. https://doi.org/10.1016/j.aquabot.2007.08.007

Martin G, Coetzee J (2014) Competition between two aquatic macrophytes, Lagarosiphon major (Ridley) Moss (Hydrocharitaceae) and Myriophyllum spicatum Linnaeus (Haloragaceae) as influenced by substrate sediment and nutrients. Aquatic Botany 114: 1–11. https://doi.org/10.1016/j.aquabot.2013.11.001

Milchunas D, Noy-Meir I (2002) Grazing refuges, external avoidance of herbivory and plant diversity. Oikos 99(1): 113–130. https://doi.org/10.1034/j.1600-0706.2002.990112.x

Mormul R, Thomaz S, Jeppesen E (2020) Do interactions between eutrophication and CO2 enrichment increase the potential of elodeid invasion in tropical lakes? Biological Invasions 22(9): 2787–2795. https://doi.org/10.1007/s10530-020-02284-8

Murphy S, Vyas D, Hoffman J, Jenck C, Washburn B, Hunnicutt K, Davidson A, Andersen J, Bennet R, Gifford A, Herrera M, Lawler B, Lorman S, Peacock V, Walker L, Watkins E, Wilkinson L, Williams Z, Tinghitella R (2021) Streetlights positively affect the presence of an invasive grass species. Ecology and Evolution 11(15): 10320–10326. https://doi.org/10.1002/ece3.7835

Oldroyd G, Leyser O (2020) A plant's diet, surviving in a variable nutrient environment. Science 368(6486): eaba0196. https://doi.org/10.1126/science.aba0196

Pearse I, Altermatt F (2013) Predicting novel trophic interactions in a non-native world. Ecology Letters 16(8): 1088–1094. https://doi.org/10.1111/ele.12143

Pearse I, Sofaer H, Zaya D, Spyreas G (2019) Non-native plants have greater impacts because of differing per-capita effects and nonlinear abundance–impact curves. Ecology Letters 22(8): 1214–1220. https://doi.org/10.1111/ele.13284

Pinheiro J, Bates D, Team R (2023) nlme: Linear and Nonlinear Mixed Effects Models.

Reid A, Carlson A, Creed I, Eliason E, Gell P, Johnson P, Kidd K, MacCormack T, Olden J, Ormerod S, Smol J, Taylor W, Tockner K, Vermaire J, Dudgeon D, Cooke S (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews of the Cambridge Philosophical Society 94(3): 849–873. https://doi.org/10.1111/brv.12480

Ren G, Li Q, Li Y, Li J, Opoku Adomako M, Dai Z, Li G, Wan L, Zhang B, Zou C, Ran Q, Du D (2019) The enhancement of root biomass increases the competitiveness of an invasive plant against a co-occurring native plant under elevated nitrogen deposition. Flora 261: 151486. https://doi.org/10.1016/j.flora.2019.151486

Ricker W (1954) Stock and Recruitment. Journal of the Fisheries Research Board of Canada 11(5): 559–623. https://doi.org/10.1139/f54-039

Sanders D, Frago E, Kehoe R, Patterson C, Gaston K (2021) A meta-analysis of biological impacts of artificial light at night. Nature Ecology & Evolution 5(1): 74–81. https://doi.org/10.1038/s41559-020-01322-x

Sardans J, Grau O, Chen HYH, Janssens IA, Ciais P, Piao S, Peñuelas J (2017) Changes in nutrient concentrations of leaves and roots in response to global change factors. Global Change Biology 23(9): 3849–3856. https://doi.org/10.1111/gcb.13721

Schaffner U, Steinbach S, Sun Y, Skjøth C, de Weger L, Lommen S, Augustinus B, Bonini M, Karrer G, Šikoparija B, Thibaudon M, Müller-Schärer H (2020) Biological weed control to relieve millions from Ambrosia allergies in Europe. Nature Communications 11(1): 1745. https://doi.org/10.1038/s41467-020-15586-1

Segrestin J, Mondy N, Boisselet C, Guigard L, Lengagne T, Poussineau S, Secondi J, Puijalon S (2021) Effects of artificial light at night on the leaf functional traits of freshwater plants. Freshwater Biology 66(12): 2264–2271. https://doi.org/10.1111/fwb.13830

Shan L, Oduor A, Liu Y (2023) Herbivory and elevated levels of CO2 and nutrients separately, rather than synergistically, impacted biomass production and allocation in invasive and native plant species. Global Change Biology 29(23): 6741–6755. https://doi.org/10.1111/gcb.16973

Shan L, Oduor A, Huang W, Liu Y (2024) Nutrient enrichment promotes invasion success of alien plants via increased growth and suppression of chemical defenses. Ecological Applications 34(1): e2791. https://doi.org/10.1002/eap.2791

Sinha E, Michalak A, Balaji V (2017) Eutrophication will increase during the 21st century as a result of precipitation changes. Science 357(6349): 405–408. https://doi.org/10.1126/science.aan2409

Slate M, Matallana-Mejia N, Aromin A, Callaway R (2022) Nitrogen addition, but not pulse frequency, shifts competitive interactions in favor of exotic invasive plant species. Biological Invasions 24(10): 3109–3118. https://doi.org/10.1007/s10530-022-02833-3

Speißer B, Liu Y, van Kleunen M (2021) Biomass responses of widely and less-widely naturalized alien plants to artificial light at night. Journal of Ecology 109(4): 1819–1827. https://doi.org/10.1111/1365-2745.13607

Sun J, Liu M, Tang K, Tang E, Cong J, Lu X, Liu Z, Feng Y (2023) Advantages of growth and competitive ability of the invasive plant Solanum rostratum over two co-occurring natives and the effects of nitrogen levels and forms. Frontiers in Plant Science 14: 14. https://doi.org/10.3389/fpls.2023.1169317

Team R (2022) R: A Language and Environment for Statistical Computing.

Uddin M, Robinson R (2018) Can nutrient enrichment influence the invasion of Phragmites australis? The Science of the Total Environment 613–614: 1449–1459. https://doi.org/10.1016/j.scitotenv.2017.06.131

Van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13(2): 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

van Kleunen M, Dawson W, Bossdorf O, Fischer M (2014) The more the merrier: Multi-species experiments in ecology. Basic and Applied Ecology 15(1): 1–9. https://doi.org/10.1016/j.baae.2013.10.006

Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. Oikos 105(2): 229–238. https://doi.org/10.1111/j.0030-1299.2004.12682.x

Vilà M, Espinar J, Hejda M, Hulme P, Jarošík V, Maron J, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14(7): 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Wang Y, Müller-Schärer H, van Kleunen M, Cai A, Zhang P, Yan R, Dong B, Yu F (2017) Invasive alien plants benefit more from clonal integration in heterogeneous environments than natives. The New Phytologist 216(4): 1072–1078. https://doi.org/10.1111/nph.14820

Wang Y, Chen X, Liu J, Hong Y, He Q, Yu D, Liu C, Dingshanbayi H (2019) Greater Performance of Exotic Elodea nuttallii in Response to Water Level May Make It a Better Invader Than Exotic Egeria densa During Winter and Spring. Frontiers in Plant Science 10: 10. https://doi.org/10.3389/fpls.2019.00144

Wang T, Yang X, Ouyang S, Huang W, Ma G, Liu S, Zhu Y, Zhang Y, Li H, Yu H (2024) The native submerged plant, Hydrilla verticillata outperforms its exotic confamilial with exposure to polyamide microplastic pollution: Implication for wetland revegetation and potential driving mechanism. Aquatic Toxicology (Amsterdam, Netherlands) 273: 107029. https://doi.org/10.1016/j.aquatox.2024.107029

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. https://doi.org/10.1007/978-3-319-24277-4_9

Wu H, Ding J (2019) Global Change Sharpens the Double-Edged Sword Effect of Aquatic Alien Plants in China and Beyond. Frontiers in Plant Science 10: 10. https://doi.org/10.3389/fpls.2019.00787

Yan Y, Oduor A, Li F, Xie Y, Liu Y (2024) Opposite effects of nutrient enrichment and an invasive snail on the growth of invasive and native macrophytes. Ecological Applications 34(1): e2737. https://doi.org/10.1002/eap.2737

Zhang Z, van Kleunen M (2019) Common alien plants are more competitive than rare natives but not than common natives. Ecology Letters 22(9): 1378–1386. https://doi.org/10.1111/ele.13320

Zhang H, Chang R, Guo X, Liang X, Wang R, Liu J (2017) Shifts in growth and competitive dominance of the invasive plant Alternanthera philoxeroides under different nitrogen and phosphorus supply. Environmental and Experimental Botany 135: 118–125. https://doi.org/10.1016/j.envexpbot.2016.12.014

Zhang X, van Kleunen M, Chang C, Liu Y (2023a) Soil microbes mediate the effects of resource variability on plant invasion. Ecology 104(10): e4154. https://doi.org/10.1002/ecy.4154

Zhang X, Zhang T, Liu Y (2023b) Effects of arbuscular mycorrhizal fungi on plant invasion success driven by nitrogen fluctuations. Journal of Applied Ecology 60(11): 2425–2436. https://doi.org/10.1111/1365-2664.14505

Supplementary material 1

Supplementary information

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Data type: docx

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